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Density-associated recruitment mediates coral population dynamics on a coral reef

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Abstract

Theory suggests that density-associated processes can modulate community resilience following declines in population size, and here we show their presence in two scleractinian populations on the outer reef of Moorea, French Polynesia, which are rapidly increasing in population size following the effects of two catastrophic disturbances. Between 2006 and 2010, 93% of the coral cover was killed by crown of thorns sea stars, in 2010 the dead coral skeletons were removed by a cyclone, and in 2011 and 2012 high coral recruitment initiated community recovery. Coral recruitment was associated with coral cover, with the relationship differing between two coral genera that are almost exclusively broadcast spawners in Moorea. Acroporids recruited at low densities, and were positively association with cover of *Acropora*, whereas pocilloporids recruited at high densities, and were negative association with cover of *Pocillopora*. Our results show there are conditions favoring recovery of contemporary corals reefs following large disturbances, specifically to promote rapid increases in population size through recruitment that is associated with coral abundance. Because these relationships differ in direction between two common and important genera of corals, they can mediate temporal shifts in taxonomic composition of coral communities.

Key words: Density dependence; recovery; Scleractinia; synecology; French Polynesia.

Introduction

Density dependence affects a wide variety of mechanisms structuring populations and communities, with positive and negative dependence accelerating or impeding (respectively) biological processes as population density increases (Courchamp et al. 1999). Recruitment is often affected by density dependence, with positive effects arising from the enhancement of population-level fecundity and recruitment by high densities of adults, and negative effects arising from conspecific interactions such as competition (Hixon et al. 2002). While most examples of density dependence are statistical reflections of the association between population density and demographic rates (Warner and Hughes 1988), their ecological value lies in the insights they provide into the causal relationships between these properties, particularly in the extent to which they affect population regulation (Hixon et al. 2002).

Evaluating the impacts of disturbances on community structure is a central goal of ecology, and disturbance effects therefore are deeply engrained in ecological theory (Pickett et al. 1989; Nystrom et al. 2000). In recent years however, especially on coral reefs, investigations have focused more keenly on disturbances linked to climate change, and the possible dramatic outcomes of such effects (Bellwood et al. 2004). In ecological theory, the increased prevalence of large changes in the community structure of coral reefs implies that regulatory mechanisms preventing such change now are less well developed than once was the case, and moreover, they suggest that once changes in community structure are initiated, they tend to be extreme. In other words, the stability and resilience of coral communities may have declined in recent decades (Nystrom et al. 2000).

Declines in coral cover are common throughout the tropics (Bruno and Selig 2007, Schutte et al. 2010; Jackson et al. 2014), but only a few reefs in recent times have been found to recover following major disturbances (e.g., Adjeroud et al. 2009; Graham et al. 2011; Gilmour et al. 2013). Poor recruitment of scleractinian corals has been proposed as a leading reason for incomplete population recovery following major disturbances (Arnold and Steneck 2011; Gilmour et al. 2013), but this outcome could be a result of multiple processes acting on one or more coral life stages. Disturbances and the recovery of coral communities are normal aspects of the biology of coral reefs (Pearson 1981; Nystrom et al. 2000), and when such events are coincident with long-term ecological studies, there is the opportunity to use them as “natural experiments” to study the processes associated with the development of coral communities. The outer reefs of Moorea, French Polynesia (Fig. 1a), provide such an opportunity, because their ecological history is particularly well known (e.g., Galzin and Pointier 1985; Berumen and Pratchett 2006; Adjeroud et al. 2009; Adam et al. 2011). Most recently these reefs suffered catastrophic damage from crown of thorns sea stars over 2006–2009 (Kayal et al. 2012), and then were impacted by a cyclone in 2010 (Adam et al. 2011). Based on sampling conducted in 2015, it is clear that these communities are recovering exceptionally quickly (described below).

Here we describe the population dynamics underlying the rapid recovery of the coral community on the outer reef of Moorea, and show that the recovery is driven by recruitment of *Pocillopora* and *Acropora* that are some of the most abundant corals in the Indo-Pacific (Veron 2000), including Moorea (Adjeroud et al. 2009). On the outer reefs of Moorea, broadcast spawning characterizes all the *Acropora* and most of the *Pocillopora* (Sier and Olive 1994; Harrison and Wallace 1990; Magalon et al. 2005; Carroll and Harrison 2006), and while the brooding coral *P. damicornis* (Richmond 1987; Fan et al. 2002) is found in Moorea, it is rarely encountered on the outer reefs. Our analyses reveal strong associations between densities of early life stages (recruits and juvenile colonies) and overall coral cover, suggesting that density dependence could serve as a mechanism mediating recruitment of these genera and ultimately, population recovery. We discuss the potential roles of such effects in determining the community structure of scleractinians as the reefs of Moorea recover from two major disturbances.

Materials and Methods

Overview

Given the local- and region- scale importance of *Pocillopora* and *Acropora* in the tropical Pacific, we focused on their populations in Moorea using data collected at the Moorea Coral Reef, Long-Term Ecological Research site (http://mcr.lternet.edu). These data describe the percentage cover of corals (2005 to 2014), the density of juvenile corals (colonies ≤ 40-mm diameter from 2005 to 2014), and the abundance of coral recruits on settlement tiles (2008 to 2014), and together we use them to describe community dynamics on the outer reef before and after two major disturbances that unfolded over several years. These data were used to explore the statistical signal of the relationships between population size and a demographic property (here, recruitment), and using these results, we evaluate the possibility that causal processes arising from organism interactions regulate local population size of *Pocillopora* and *Acropora*.

The most recent disturbances affecting the outer reefs (10-12 m depth) of Moorea prior to 2006, were bleaching and a cyclone in 1991 that reduced coral cover to 22.5%, and bleaching in 1994, 2002, and 2003 that ultimately had little impact on coral cover (Adjeroud et al. 2009). By 2005 however, at 10-m depth on the outer reef, coral covered 38 ± 2% (mean ± SE, n = 6 sites) of the benthos (Adam et al. 2011), with *Pocillopora* and *Acropora* the dominant coral genera (37% of the coral; http://mcr.lternet.edu). By 2006, high population densities of the corallivorous seastar *Acanthaster planci* were recorded on the reefs of Moorea (Kayal et al. 2012), and by 2009 they had reduced coral cover on the outer reef to 10 ± 4% (mean ± SE, n = 6 sites) (Adam et al. 2011; Kayal et al. 2012). Waves from Cyclone Oli in February 2010 removed virtually all of the dead coral skeletons left by *A. planci* on the north shore, and surveys of these reefs in April 2010 revealed ≤ 3.4% mean coral cover at 10-m and 17-m depths (n = 40 quadrats at two sites for both depths; Fig. 1c).

Coral community structure

Starting in April 2005, coral community structure was quantified using photoquadrats (0.5 × 0.5 m) recorded in annual increments at 6 sites at 10-m depth on the outer reefs of Moorea (Fig. 1 b, c). A single 40-m transect is marked permanently at each site, and 40 photoquadrats are recorded annually at fixed positions that initially were randomly selected. Images were analyzed using CPCe software (Kohler and Gill 2006) with 200 dots (10 pixel diameter) randomly placed on each image, and under which scleractinians (and *Millepora*) were scored to genus and quantified as percentage cover. Island-wide trends in coral community structure were described using sites as replicates (n = 6, with 2 sites on each of the three shores) and three categories of benthic organism of direct relevance to the present analysis: overall cover of scleractinians, cover of *Pocillopora* and cover of *Acropora*.

The population dynamics of *Pocillopora* and *Acropora* were described in detail using two sites (LTER 1 and 2) on the north shore of Moorea (Fig 1a), where coral cover, the density of juvenile corals, and coral recruitment are measured with at least annual resolution. The sites on the southeast and southwest shores were not included in this portion of the analysis, as sampling is more limited in these locations that are less accessible from the marine laboratory where our research is based. In this portion of the analysis, photoquadrats were treated as replicates and pooled between LTER1 and LTER2 (n ~ 80 y^{-1}). To place the changes in populations of *Pocillopora* and *Acropora* at these two sites in a broader context, specifically the extent to which the coral community have recovered since the *Acanthaster planci* outbreak and Cyclone Oli, the among-year similarity in the coral communities (scleractinian and *Millepora*) at LTER1 and LTER2 was described with genus resolution for 10 years using non-metric multidimensional scaling (MDS).

Juvenile corals

Starting in April 2005, juvenile corals ≤ 40-mm diameter were quantified in situ to genus, using 0.5 × 0.5 m quadrats placed at the same positions as the photoquadrats. Fragments generated by breakage were excluded by focusing on juvenile colonies that had a clear basal attachment to the substratum without fractured edges or dead portions. Likewise, fission products were avoided by counting small colonies that were composed of new skeleton rather than portions of an antecedent framework.

Coral recruits

Coral recruits were assayed using unglazed terracotta tiles (15 × 15 × 1 cm) secured individually at 10-m depth at the two north shore sites (LTER 1 and 2) (similar to Edmunds et al. 2010). At each site, fifteen tiles were attached independently to the reef with a ~ 1 cm microhabitat beneath and each tile positioned approximately horizontal. Tiles were first deployed at 10 m depth on the outer reef in January 2007, and thereafter were exchanged in August/September and January/February. They were bleached, dried, and scored on all surfaces (top, bottom, and edges) for coral recruits that were identified to family. Pocilloporids in Moorea are represented by one genus, while acroporids are represented by *Acropora* spp., *Astreopora* spp., and *Montipora* spp. *Astreopora* spp. and *Montipora* spp. have typically occurred at relatively low cover on the outer reefs (Adjeroud et al. 2009; Edmunds et al. 2010). For *Acropora* spp. and *Pocillopora* spp. therefore, recruits identified to family are likely to provide an effective estimate of the additions through sexual reproduction of new individuals to support population growth of these two genera. To estimate annual coral recruitment, mean recruit densities at each of two samplings per year (n = 30 tiles sampling^{-1}, pooled between sites, from 2008 to 2014) were summed (corals tile^{-1} y^{-1} based on ~ 60 tiles).

Data analysis

To test for changes over time in cover of corals and density of juvenile corals one-way repeated measures ANOVA (RM-ANOVA) were used in which Time was the main (repeated) factor with 10 levels (from 2005 to 2014), coral cover (arcsin transformed) and density of juvenile corals were the dependent variables (in separate univariate tests), and photoquadrats (~ 80 year^{-1}) were the statistical replicates. RM-ANOVAs were performed using R software (package "ez", command "ezANOVA").

As settlement tiles were exchanged in August/September and January/February, annual recruitment was estimated by summing the mean density of recruits across both sampling periods within each year. Each measure of recruitment therefore was based on the number of recruits encountered on two batches of ~ 30 tiles y^{-1}. This procedure was necessary to evaluate recruitment that occurred within the minimal sampling interval for coral cover and density of juvenile corals (i.e., 1 year), but it had the limitation of providing no measure of error and precluded inferential analyses of annual recruitment. To test for changes in density of recruits over time, an inferential test was applied to the single sampling period in each year with the highest recruitment (August/September), when individual settlement tiles could be used as statistical replicates. Using this subset of recruitment data, one-way ANOVA (R software, command "aov") was used to test for differences in recruitment over time (7 years between 2008 and 2014) using the density of acroporid and pocilloporid recruits as dependent variables in separate univariate analyses. For the analyses of adult coral cover, and density of both juvenile corals and recruits, when the main effect of Time was statistically significant, post hoc analyses were performed using either pairwise comparisons (for RM-ANOVA) or Tukey HSD test (for the one-way ANOVA). For all statistical tests, the assumptions of normality and homoscedasticity were evaluated through graphical analysis of residual. For RM-ANOVA, the assumption of sphericity was verified by Mauchly test. When the Mauchly test was significant (i.e., the null hypothesis of sphericity was rejected), a Greenhouse-Geisser correction was applied to the data.

To place the population dynamics of *Pocillopora* and *Acropora* over 2005–2014 in a broader context of changes in the overall coral community, the similarity among years based on coral cover by genus and site (LTER1 and LTER2) was evaluated within a MDS framework using Primer-E v 6 software (Clarke and Gorley 2006). In this analysis, coral cover was log(x + 1) transformed, similarities among years evaluated by the method of Bray-Curtis, and the results displayed with MDS using multiple restarts of 100 iterations until stress stabilized and ordinations were repeatable.

We tested for density-association phenomena by exploring the relationships among coral cover and the density of both juvenile and recruiting corals as determined using data collected over multiple years (i.e., a time-series). The analyses of time-series data are prone to artifacts arising from autocorrelation, and in tests of temporal trends and associations between two time series, these effects can elevate the risks of Type I errors and create biases in describing the linear relationships between variables (Bence 1995). Prior to testing for density association, we therefore tested for autocorrelation using a Durbin-Watson procedure (implemented in R software, command “dw.test”). As none of the time series data were significantly autocorrelated ($P > 0.05$), density association was evaluated using Pearson correlations to test for relationships between coral cover (a proxy for population size) and the densities of juvenile corals and coral recruits (annualized). Separate analyses were conducted for *Pocillopora* spp. and *Acropora* spp., and where significant associations were detected the functional relations were described by Model II regression (described below).

Association between coral cover and density of early life stage corals (i.e., juveniles and recruits) was evaluated following a 3-step procedure. First the best model describing the relationship between the two random variables was chosen according to an Akaike information criterion (AIC) approach (Akaike 1978). Linear, exponential, and power models were tested for each set of data, and the model providing the lowest AIC value was chosen to provide the best description of the relationship between the variables. Second, the statistical association between the variables was evaluated using Pearson correlations and variables transformed to correspond to the relationship that best described the data (as selected by lowest AIC values). Third, where the two variables were significantly associated, the functional relationship between them was described using Model II regression techniques because of the random nature of both variables (Sokal and Rohlf 2012). In this procedure, the slope of the relationship was determined by the method of standard major axis (SMA) (Sokal and Rohlf 2012; R software, command “lmodel2”).

Pearson correlations were calculated using a 1-year lag for recruitment and a 1–2 years lag (depending on genus) for juveniles relative to the year in which adult cover was measured. For example, correlations for recruitment paired recruit density in each year with coral cover the previous year, and correlations for juveniles paired juvenile density in each year either with coral cover in the previous year (i.e., a 1 y lag for *Pocillopora spp*), or with coral cover two years before (i.e., a 2 y lag for *Acropora spp*). A lagging approach was used because we reasoned that an effect of adult population size (i.e., coral cover) on recruits and juveniles would only be detectable after the passage of sufficient time to allow these small life stages to be enumerated. The settlement tiles used to assess recruitment were deployed for ∼ 6 months at each sampling, and the recruits appearing on these times suggested a lag of 6-12 months provided a conservative estimate of the time necessary to capture the recruitment signal from each spawning event. For juvenile corals, a 2 y lag was applied to *Pocillopora* spp*.* and a 1 y lag to *Acropora* spp., because they grow at different rates. Assuming juvenile *Pocillopora spp*. grow at ~ 2 cm y^{-1} (Bramanti et al. 2015; Pratchett et al. 2015), a 2 y lag therefore provides a conservative means to test for an association between the density of juveniles and coral cover. Juvenile *Acropora* spp. grow faster (i.e., ~ 4 cm y^{-1} [Pratchett et al. 2015]) than juvenile *Pocillopora* spp., and therefore the relationship between the density of juvenile *Acropora* spp. and coral cover was tested with a 1 y time lag.

Results

Community recovery

In 2005, mean coral cover (averaged across 6 sites on 3 shores) at 10 m depth on the outer reefs of Moorea was 40%, with 20% cover of *Pocillopora* spp. and 10% cover of *Acropora* spp. (Fig. 3a). In 2011, after major disturbances affecting these reefs (*Acanthaster planci* outbreak [Kayal et al. 2012] and Cyclone Oli [Adam et al. 2011]), the lowest mean coral cover detected in this study was recorded (2.7%; Fig 3a). By 2012, mean coral cover had increased to 4.0%, and the increase intensified in 2014 (when mean coral cover reached 26.3%). The increase in coral cover from 2012 to 2014 was mainly driven by *Pocillopora* spp., which increased in mean cover from 1.8% (2012) to 17.6% (2014), whereas mean *Acropora* spp. cover remained < 1%.

In a broader context, the MDS plots displaying coral community structure based on mean coral cover by genus at LTER1 and LTER2 (both on the north shore) revealed the large extent to which the community was perturbed from 2005 to 2010, and the high degree to which it had recover by 2014 (Fig. 2). Relative to the coral community structure in 2005 as evaluated by the Bray Curtis similarity, by 2014 the community was 68% similar to the initial condition at LTER1, and 70% similar at LTER2.

Pocillopora population

For *Pocillopora* spp. (Fig. 3b, left panel), cover changed over time (RM-ANOVA, $F_{9,711}$ = 256, $p < 0.001$), with no change between 2005 and 2007 (pairwise comparison: 2005 = 2006, 2006 = 2007, 2005 = 2007, all $p > 0.050$) but a decline between 2007 and 2010 (pairwise comparison: 2007 > 2008; 2008 > 2009; 2009 > 2010, all $p < 0.001$). *Pocillopora* cover did not change between 2010 and 2011 ($p > 0.050$), but it increased between 2011 and 2014 (pairwise comparison: 2011 < 2012, $p < 0.001$; 2012 < 2013, $p < 0.001$; 2013 < 2014, $p < 0.001$). For juvenile *Pocillopora* spp., densities varied over time (RM-ANOVA, $F_{9,711}$ = 250, $p < 0.001$), with no change between 2005 and 2010 (pairwise comparison: 2005 = 2006 = 2007 = 2008 = 2009 = 2010, all $p > 0.05$) but an increase following 2010 when the lowest cover of *Pocillopora* spp. was recorded (pairwise comparison: 2010 < 2011; 2011 < 2012, all $p < 0.001$). In 2013 and 2014, the density of juvenile *Pocillopora* spp. decreased relative to 2012 (pairwise comparison: 2012 > 2013 > 2014, $p < 0.001$). For pocilloporid recruits, densities recorded in August/September differed among years (ANOVA, $F_{6,206}$ = 4.29, $p < 0.01$), with similar densities in 2008 and 2010, an increase from 2011 to 2012, and a decrease in 2013 and 2014 (Tukey HSD, 2008 = 2009 = 2010 , $p > 0.050$; 2010 < 2011, $p < 0.001$; 2011 < 2012, $p < 0.001$; 2012 > 2013 > 2014, $p < 0.001$).

For *Pocillopora* spp., the AIC analyses showed that the relationship between adult cover and density of coral recruits was best described by a power curve, and the relationship between adult cover and the density of juvenile corals by a negative exponential relationship (Table 1). Pearson correlations revealed a significant negative relationship between coral cover and the density of recruits (for Log-Log transformed data, $r = -0.83$, $df = 5$, $p < 0.05$), and between coral cover and density of juvenile colonies (for Log-Linear transformed data, $r = -0.97$, $df = 6$, $p < 0.01$). Model II regression provided the best-fit lines describing the functional relationships between these variables, with the exponent for the power curve (i.e., the slope on linearized axes for recruits on cover) having a value of - 0.45 (Fig 3b, right panel), and constant in the exponential relationship (i.e., the slope on linearized axes for juveniles on cover) having a value of -0.93 (Fig 3b, right panel).

The lowest *Pocillopora* spp. cover in 2010 (0.2%) was followed in 2011 by a high density of pocilloporid recruits (6.7 corals tile^{-1}), and in 2012 the highest density of recruits was recorded (8.2 corals tile^{-1}; Fig. 3b, left panel). Likewise, the highest density of juvenile *Pocillopora* spp. (12.6 juveniles 0.25 m^{-2}; Fig. 3b, left panel) was recorded in 2012, 2 y after the cover of this genus was at a minimum. As density of recruits and juvenile colonies was negatively associated with *Pocillopora* spp. cover (Fig. 3b, right panel), recruitment began in earnest when this coral virtually was extirpated from the outer reef. Increased *Pocillopora* spp. cover in 2012 (from 0.33% to 2.07%) and 2013 (from 2.07% to 7.30%) was followed in 2013 and 2014 by decrease in density of recruits (from 8.29 to 0.67 corals tile^{-1}) and juveniles (from 12.62 to 4.74 juveniles 0.25 m^{-2}).

Acropora population

For *Acropora* spp. (Fig 3c, left panel), cover changed over time (RM-ANOVA, $F_{9,711} = 227.3$, $p < 0.001$), with similar cover from 2005 and 2007 (pairwise comparison: 2005 = 2006 = 2007, $p > 0.05$) and decreases between 2007 and 2009 (pairwise comparison: 2007 > 2008; 2008 > 2009, all $p < 0.001$). Between 2009 and 2011, *Acropora* spp. cover remained at ~ 0.02% (pairwise comparison: 2009 = 2010 = 2011; $p > 0.050$), but gradually increased in the following 3 years (pairwise comparison: 2011 < 2012 < 2013 < 2014, $p < 0.001$). The density of juvenile *Acropora* spp. differed among years (RM-ANOVA, $F_{9,711} = 250.1$, $p < 0.001$), with changes among years that were similar to those affecting the cover of *Acropora* spp. from 2005 to 2009 (pairwise comparison: 2005 = 2006 = 2007, $p > 0.050$; 2007 > 2008, $p < 0.001$; 2008 > 2009, $p < 0.001$). A decrease in density of *Acropora* spp. juveniles occurred from 2009 to 2010 (pairwise comparison: 2009 > 2010, $p < 0.001$) followed by an increase from 2010 to 2012 (pairwise comparison: 2010 < 2011 < 2012, $p < 0.001$). From 2012 to 2014, density of *Acropora* spp. juveniles gradually decreased (pairwise comparison: 2012 > 2013 > 2014, $p < 0.01$). For acroporid recruits, densities recorded in August/September differed among years (ANOVA, $F_{6206} = 4.06$, $p < 0.001$), but post hoc analyses showed that this effect was due to high recruitment in 2012 (TukeyHSD, 2008 = 2009 = 2010 = 2011, $p > 0.050$; 2011 < 2012, $p < 0.001$; 2012 > 2013, $p < 0.001$; 2013 =2014, $p > 0.05$).

Like *Pocillopora*, *Acropora* spp. was effectively removed from the outer reef by 2010 (cover < 0.01%), but unlike *Pocillopora*, densities of *Acropora* spp. juveniles and acroporid recruits have remained low in the following years (mean values of 0.21 juveniles 0.25 m^{-2} $y^{-1}$and 0.68 recruits $tile^{-1}$ y^{-1}, respectively). Although acroporid recruits were found at a relatively high mean density of 1.65 corals $tile^{-1}$ in 2012, in 2014 the density of juvenile *Acropora* spp. and acroporids recruits both were low (0.10 m^{-2} and 0.27 corals $tile^{-1}$, respectively) (Fig. 3c, left panel).

For *Acropora* spp., the AIC analysis showed that the relationships between adult cover and density of coral recruits and juveniles were best described by power, curves (Table 1). However, the association between coral cover and density of recruits was not significant (for

Log-Log transformed data, $r = 0.29$, $df = 5$, $p > 0.1$), although the association between coral cover and density of juveniles was significant (for Log-Log transformed data, $r = 0.96$, $df = 7$, $p < 0.01$). Model II regression described the-best fit functional relation for juvenile density on coral cover with a power curve having an exponent of 0.41 (Fig 3c, right panel).

Discussion

We investigated the dynamics of an ongoing recovery of a coral community on the outer reef of Moorea after disturbances reduced coral on the outer reef > 92% (from 38% in 2005 to 3% in 2011). Using census data, we quantified recruitment of *Pocillopora* spp. and *Acropora* spp., the two most abundant coral genera on the outer reefs of Moorea, with the objective of describing the dynamics of coral community staging a remarkable recovery from catastrophic damage. The broad-reaching scope of this recovery is revealed by the overall coral cover in 2014 relative to 2005, the cover of the two dominant genera (*Acropora* and *Pocillopora*) over the same period, and a strong trend towards restoration of the full generic coral composition (for scleractinians and *Millepora*) in 2014 relative to 2005. By focusing on *Pocillopora* spp. and *Acropora* spp. during this recovery period we were able to contrast two important genera that share a spawning reproductive strategy, but which differ in reproductive timing in this location. *Pocillopora* spp. reproduces during an extended period lasting several months (Gleason 1996; Adjeroud et al. 2007; Edmunds et al. 2010) whereas *Acropora* spp spawns in a discrete mass spawning event (Carroll and Harrison 2006). Our results show different directions of density association between coral cover and both recruits and juveniles in these two genera, which may be associated with their contrasting reproductive phenologies.

Our study cannot test for cause-and-effect relationships that drive the density association we report, however the associations are consistent with the hypothesis that different density-dependent relationships (positive or negative) involving recruitment of *Pocillopora* spp. and *Acropora* spp. modulate the recovery of coral populations on this outer coral reef community. For *Pocillopora* spp., our results show a negative association between cover and density of recruits, which is consistent with a causal mechanism involving negative density dependence modulating recruitment of *Pocillopora* spp. In contrast, for acroporids we found a positive association between cover and density of juveniles, which is consistent with a causal mechanism involving positive density-dependence modulating recruitment of *Acropora* spp. While there was no association between cover and density of recruits this outcome may reflect the low density of recruits of this genus (< 1.65 recruit tile^{-1}), and the limited capacity of the small target areas of settlement tiles to detect them. Different reproductive strategies, as shown by *Acropora* spp. and *Pocillopora* spp. in Moorea, can result in different recovery dynamics following major disturbances, and understanding the mechanisms mediating these dynamics is likely to be one important part of the puzzle in determining the coral community structure of future reefs. On coral reefs in the Indo-Pacific, *Pocillopora* spp. and *Acropora* spp. are characterized by different life history strategies, with *Pocillopora* spp. generally having a high population turnover and *Acropora* spp. showing slower population dynamics (Darling et al. 2012). Species characterized by populations with fast turnover are well known for their ability to colonize recently-disturbed habitats (Grime 1977; Grime and Pierce 2012), whereas species forming population characterized by slow dynamics tend to dominate in favorable environments, but have slow recovery capacities (Darling et al. 2012).

Our results document profound changes affecting the outer reefs of Moorea in quick succession within a decade, and describe a sequence of events that have turned a reef with high coral cover into a pavement of rock, and then back to a coral-dominated community within a few years. The recovery has been fueled by recruitment of pocilloporid and acroporid corals displaying contrasting recovery dynamics that may reflect different mechanisms of population regulation by members of these genera. Previously, recovery dynamics for coral communities on the outer reefs of Moorea have been reported (Adjeroud et al. 2009), and these are similar to the present results in describing large declines in coral cover following multiple disturbances between 1991 and 2006, followed by rapid recovery of coral cover. This earlier description of the reefs of Moorea showed that the recovered coral community differed in relative abundance of coral genera compared to that described initially (Adjeroud et al. 2009), and while this again may be the case as the reefs continue to recover, the coral community developing in the first 4 y after the most recent disturbance does not support this possibility (Fig. 2).

In Moorea, there is evidence that *Pocillopora* spp. recruits throughout much of the year (Gleason 1996; Adjeroud et al. 2007; Edmunds et al. 2010), which suggests that their larvae are the products of a lengthy period of reproduction and may be consistently present in the seawater flowing over the outer reefs. Although the brooding pocilloporid *P. damicornis* (Stoddart and Black 1985) is occasionally seen on the outer reefs of Moorea (PJ Edmunds personal observation), the majority of the pocilloporids on the outer reefs of Moorea (*P. meandrina*, *P. verrucosa*, and *P. eydouxi*) are spawners (Harrison and Wallace 1990; Sier and Olive 1994; Hirose et al. 2011; Schmidt-Roach et al. 2012). Throughout the Indo-Pacific, *P. meandrina, P. eydouxi* and *P. verrucosa* are characterized by a spawning reproductive strategy (Schmidt-Roach et al. 2012), although brooding by *P. verrucosa* has been recorded in the Phillipines (Villanueva et al. 2008), and brooding by *P. meandrina* has been recorded in Enewetak (Stimson 1978). Therefore, it is likely that the pocilloporid recruits we detected on the reefs of Moorea are the products of external fertilization with pelagic larval durations (PLD) varying from hours-to-days depending on the species (Harrison and Wallace 1990; Jones et al. 2009). Given the potential PLD of *Pocillopora* spp. larvae, the short distance between near-by islands around Moorea (e.g., Tahiti lies 17 km east), the speed of prevailing surface currents (30 – 50 cm s^{-1}, Martinez et al 2006), and the high fecundity of *Pocillopora* spp. (Sier and Olive 1994), it is likely that at least Tahiti supplies some of the *Pocillopora* spp. larvae recruiting to the reefs of Moorea (Magalon et al. 2005). Critically, however, the extent to which this inferred larval transport occurs will depend on the degree of synergy among a large number of factors including the seawater currents, the fecundity of corals in each spawning event, the exact timing and duration of the spawning event (see Kough and Paris 2015), and the availability of suitable settlement surfaces when competent larvae arrive at the reef surface. Given the serendipitous nature of the likelihood of these factors conspiring to promote the transport of coral larvae among these islands, it is possible that the connectivity signal vested in different cohorts of coral recruits could differ very greatly.

In addition to the potential for coral recruits on Moorea to originate in more distant locations (like Tahiti), *Pocillopora* spp. and *Acropora* spp. are also present in the back reef of Moorea (Edmunds et al. 2010), and colonies in this location also could provide larvae that recruit to the outer reef. Cross-reef transport of fish larvae and their delivery to the outer reef is known to occur in Moorea (Adam et al. 2011), for when the outer reef was depleted of coral in 2010, population growth of macroalgae was suppressed by the migration of parrotfish from the lagoon and back reef to the outer reef community (Adam et al. 2011). Elucidating the absolute roles of local versus more distant sources of pocilloporid and acroporid larvae in supporting coral recruitment on the outer reefs of Moorea must be a research priority to understand the extent to which population connectivity on a scale of 10's of kilometers modulates local-scale reef recovery.

On the outer reefs of Moorea and at high population densities of *Pocillopora* spp., negative density-dependent mechanisms may underlie the association between cover and recruitment. While it was beyond the scope of this study to test for a mechanistic basis to this association for *Pocillopora* spp., there are at least two possibilities that could be relevant. First, high densities of branched adult colonies could deplete waterborne resources (such as zooplankton) that are necessary to sustain downstream recruits and juvenile colonies (Kim and Lasker 1997). This effect could generate a trophic shadow (sensu Porter 1976) that deters recruitment through food limitation in downstream locations. Alternatively, upstream corals could create a "wall of mouths" (sensu Fabricius and Metzner 2004) from their numerous branches and polyps that could consume a wide diversity of planktonic organisms, including larvae. Second, it is possible that host–specific biotic interactions could cause positive density dependent mortality of coral larvae and coral recruits. This mechanism could be analogous to the ways by which, in tropical forests, pathogens on young seedlings of the tree *Shorea quadrinervis* cause highest mortality in areas of high adult density, where transmission of pathogens presumably is most likely (Blundell and Peart 2004). On coral reefs, a negative association between coral cover and the abundance of juvenile corals has been recorded for the Caribbean coral *Siderastrea radians* by Vermeij (2005), and a waterborne factor, whose effect became stronger as coral cover increased, has been hypothesized as an explanation (Vermeij and Sandin 2008). According to Marhaver et al. (2013), conspecific recruits settling downstream of the Caribbean coral *Orbicella faveolata* were negatively affected by microbial flora associated with adult colonies, resulting in a negative density dependent effect on recruitment. Conceivably, similar effects could modulate recruitment of *Pocillopora* spp. in Moorea.

Different life history traits typically drive differential recovery dynamics of populations following disturbances (Stearns 1997), and in Moorea differential timing of reproduction in *Acropora* spp. versus *Pocillopora* spp. may be important in facilitating contrasting patterns of density association in recruitment. In this location, *Acropora* spp. mass spawns between September and November (Carrol and Harrison 2006), and the highest recruitment of acroporids occurs from December to March (Adjeroud et al. 2007). In contrast, pocilloporids tend to recruit year-round on the reefs of Moorea (Gleason 1996; Adjeroud et al. 2007; Edmunds et al. 2010), suggesting that reproduction in this family is not constrained to a single period each year (Sier and Olive 1994). The trends for variation in population density reported here for *Acropora* spp. are different from those for *Pocillopora* spp. For the Acroporidae, we found positive density association based on the *Acropora* spp. cover, with the effect weak for recruits and strong for juveniles (Fig. 2c right panel). This pattern suggests that, at a local scale (i.e., < 10 km scale), recruitment may be supported by near-by adult colonies (i.e., self-seeding). This mechanism should be accentuated by the temporally constrained reproduction of *Acropora* (i.e., with September-November spawning in Moorea) that would make their larvae available for settlement during only short periods each year. Effectively, this could constrain the supply of acroporid larvae to the outer reefs of Moorea, and dampen the potential for among-island connectivity (sensu Black et al. 1991).

Together, our results underscore the potential importance of density dependence and its role in determining population size (Herrando-Pérez et al. 2012), in understanding the response of contemporary coral communities to disturbances. By exploiting this realm of ecological theory to augment our understanding of the coral communities of Moorea, we make the case that density dependence is associated with population-level responses of two coral genera to disturbances acting over the spatial scale of the present analysis. However, the implications of our results are limited by their grounding in correlation rather than cause-and-effect, and addressing this limitation is an important goal of future research. This task will not be easy however, as it will require large-scale manipulative experiments in which the density of adult corals, juvenile corals, and coral recruits are modified in an orthogonal design. Such an approach may no longer be acceptable in an era when so many coral reefs have degraded and the permitting framework for manipulative experimentation is highly restrictive. Notwithstanding the limitations of our study, our results are likely to have broad application to other coral reefs, because the genera studied are representative of large functional groups of corals having different life-history strategies (i.e., extended reproduction throughout the year versus temporally restricted reproduction). Moreover, our findings may also apply to other reefs that operate as part of larger metapopulations linked through hydrodynamic connectivity in which the likelihood of recovery following disturbances is determined, in part, by density dependent mechanisms. If the trends we describe have a mechanistic basis, then the recovery dynamics of denuded reefs may be driven by corals with life-history strategies characterized by protracted periods of reproduction and strong potential through pelagic larvae for connectivity among nearby reefs.

Acknowledgments

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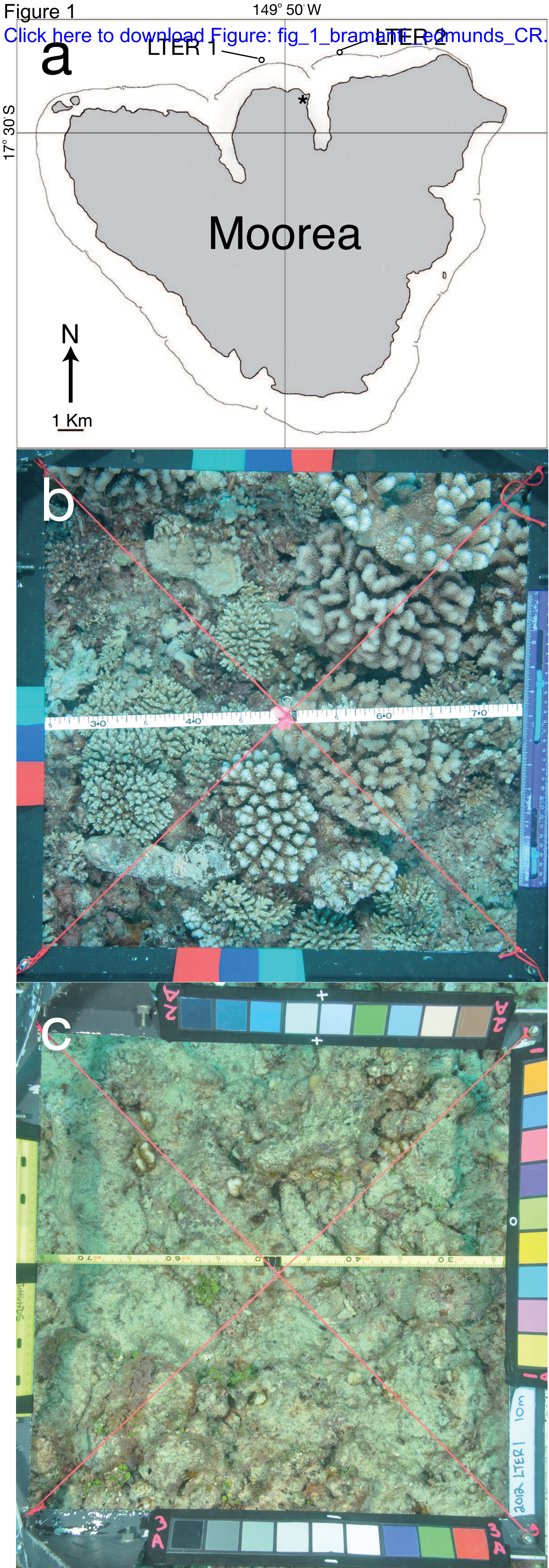
Figures legends

Fig. 1. Map of Moorea showing study sites (a) and representative photoquadrats (0.5 × 0.5 m) from 10 m depth in 2005 (b) and 2013 (c).

Fig 2. Non-metric multidimensional scaling plots showing the similarity of coral community structure among 10 years between 2005 and 2014 for LTER1 (a) and LTER2 (b), both at 10 m depth. Plots were prepared from mean coral cover by year for scleractinians and *Millepora*, that were log(x + 1) transformed prior to preparing resemblance matrices by the method of Bray Curtis; ordinations were generated from multiple restarts of 100 iterations. Bubbles for each year are scaled to show percentage cover of *Pocillopora* spp.

Fig. 3. Coral community structure from 2005 to 2014). (a) Island-wide community structure based on 6 sites (2 sites shore^{-1}; mean ± SE, n = 6); (b) Abundance of *Pocillopora* spp. on the north shore (LTER 1 and LTER2, Fig. 1). Left panel: cover (mean ± SE, left ordinate), density of juvenile colonies (mean ± SE, right ordinate), and density of recruits (summed within each year, right ordinate, 2008-2014). Right panel: relationships between cover of *Pocillopora* spp. and density of juvenile *Pocillopora* spp ($r = 0.97$, $p < 0.01$, $n = 8$)., and pocilloporid recruits ($r = 0.83$, $p < 0.05$,, $n = 7$) using a time lag of 2 y; (c) Abundance of *Acropora* spp. on the north shore (LTER 1 and LTER2). Left panel: cover (mean ± SE, left ordinate), density of juvenile colonies (mean ± SE, right ordinate), and density of acroporid recruits (summed within each year, right ordinate, 2008-2014). Right panel: relationships between cover of *Acropora* and density of juveniles ($r = 0.96$, $p < 0.01$, $n = 9$).

Figure 1


149° 50' W
a
LTER 1
LTER 2
17° 30' S
*
Moorea
N
1 Km
b
3·0
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c
2A
3A
2018 LTER1
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Figure 2

Click here to download Figure: fig_2_bramanti_edmunds_CR.eps

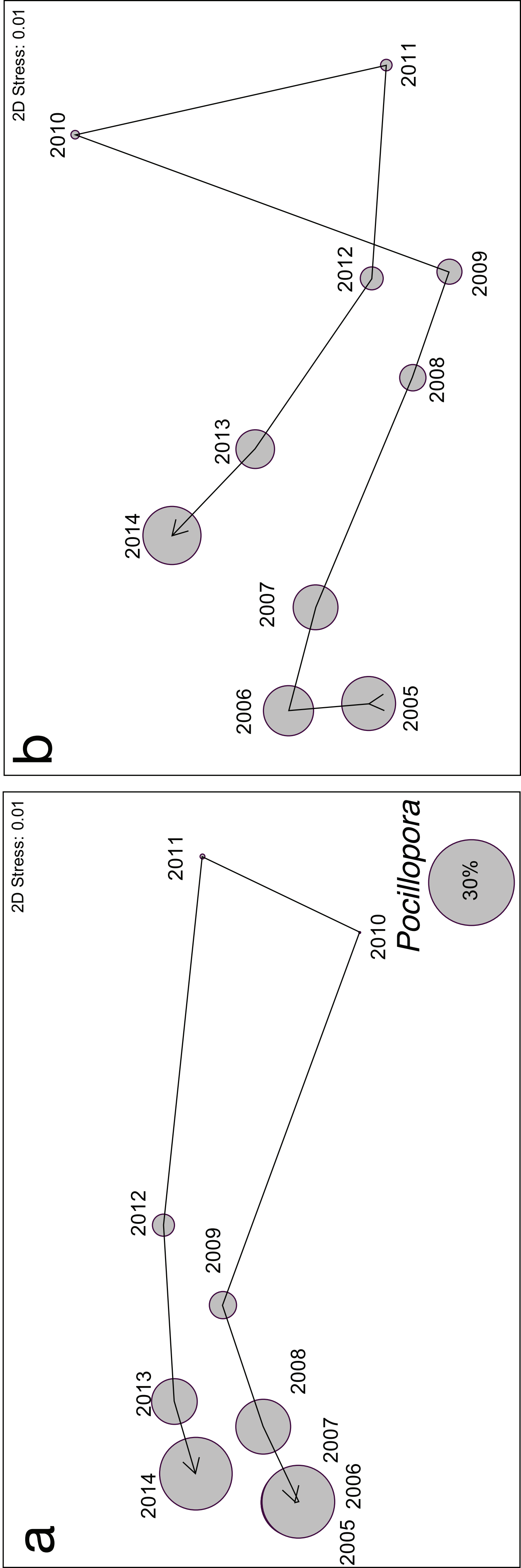

Figure 3

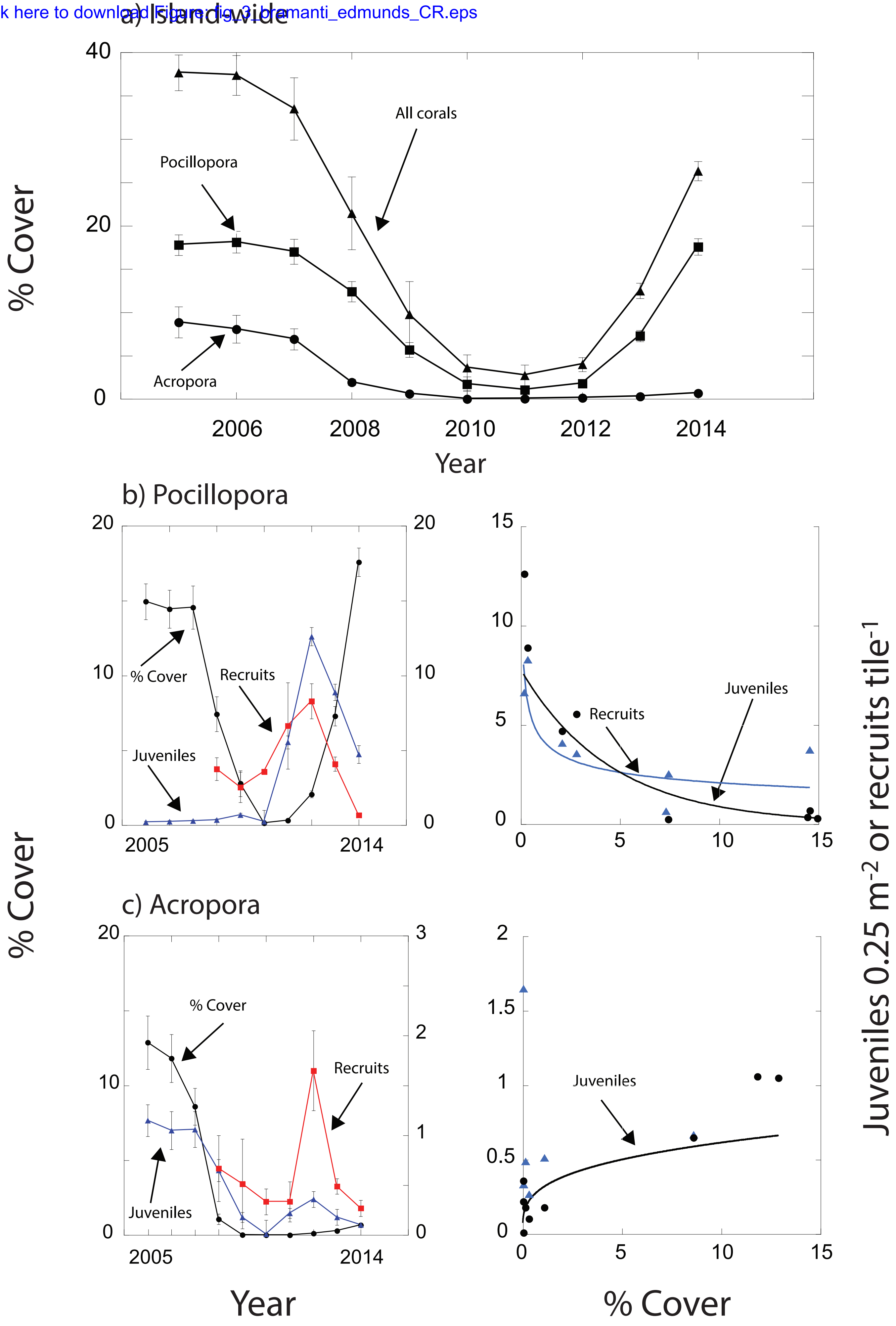
a) Islandwide
% Cover
40
20
0
2006
2008
2010
2012
2014
Year
All corals
Pocillopora
Acropora
b) Pocillopora
20
10
0
2005
2014
% Cover
Recruits
Juveniles
20
10
0
15
10
5
0
0
5
10
15
Recruits
Juveniles
c) Acropora
20
10
0
3
2
1
0
2005
2014
% Cover
Recruits
Juveniles
2
1.5
1
0.5
0
0
5
10
15
Juveniles
% Cover
Year
% Cover
Juveniles 0.25 m-2 or recruits tile-1

Table 1. Akaike Information Criterion (AIC) values for the three models tested (linear, power and exponential). The model with the lowest AIC value (in bold) was chosen to describe the relationship between adult (x axes) and recruit or juveniles (y axes) for *Pocillopora spp* and *Acropora spp*.

Genus	Dependent variab;e	**Model**	**AIC value**
Pocillopora spp.	Adults/recruits	Linear	11.8
		Power	**6.3**
		Exponential	8.7
	Adults/juveniles	Linear	22.3
		Power	15.9
		Exponential	**2.52**
Acropora spp.	Adults/recruits	Linear	-8.55
		Power	**-9.23**
		Exponential	-8.59
	Adults/juveniles	Linear	-38.5
		Power	**-39.3**
		Exponential	-31.2